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Strønen, Astrid Vik; Iacolina, Laura; Ruiz-González, Aritz

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Review Paper

Rewilding and conservation genomics: How developments in (re)colonization ecology and genomics can offer mutual benefits for understanding contemporary evolution

Astrid Vik Stronen ^{a, b, c, *}, Laura Iacolina ^{c, d, e}, Aritz Ruiz-Gonzalez ^f

^a Department of Biology, Biotechnical Faculty, University of Ljubljana, Večna pot 111, 1000, Ljubljana, Slovenia

^b Department of Biotechnology and Life Sciences, Insubria University, via J.H. Dunant 3, 21100, Varese, Italy

^c Department of Chemistry and Bioscience, Aalborg University, Fredrik Bajers Vej 7H, 9220, Aalborg, Denmark

^d Aalborg Zoo, Mølleparkvej 63, 9000, Aalborg, Denmark

^e Department of Fisheries, Beekeeping, Game Management and Special Zoology, Faculty of Agriculture, University of Zagreb, Svetošimunska cesta 25, 10000, Zagreb, Croatia

^f Department of Zoology and Animal Cell Biology, University of the Basque Country UPV/EHU, C/ Paseo de la Universidad 7, 01006, Vitoria-Gasteiz, Spain

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ABSTRACT

A 'rewilding' process is occurring in Europe and beyond, centered on landscapes reverting from agricultural use to a more natural state. Wild species are arriving by natural or human-mediated range expansion, at times reclaiming ranges from which they were lost centuries ago. Recent colonizers include alien invasives and species expanding their historical distribution without direct human assistance. These events can deepen our understanding of contemporary evolution, including wildlife responses to changing climatic conditions. Rewilding can advance conservation genomics by encouraging study of wildlife in environments where these species represent novel arrivals or return after prolonged absences. Such efforts could facilitate more experimental approaches to research design than that typically feasible for landscape-scale ecological and evolutionary studies. Correspondingly, developments in conservation genomics offer unparalleled means for testing predictions about rewilding, and advancing evolutionary enlightened and proactive conservation planning. In this perspective article, we examine four European carnivore species relevant as case studies of (re)colonization and/or rewilding, and discuss examples of emerging research opportunities in genomics, evolutionary ecology, and human-wildlife relationships.

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1. Introduction

In Europe and beyond, landscapes altered by humans are experiencing a "rewilding" process, with large areas reverting to a more naturalized state (Pereira and Navarro, 2015), thus promoting a (re)colonization process by wild species (Deinet et al., 2013) including wide-ranging carnivores (Chapron et al., 2014). Several forces facilitate this process, including abandonment of marginal agricultural areas and growing urbanization, changing social attitudes to wildlife, and improved legal protection

* Corresponding author. Department of Biology, Biotechnical Faculty, University of Ljubljana, Večna pot 111, 1000, Ljubljana, Slovenia.

E-mail addresses: astrid.stronen@gmail.com (A.V. Stronen), lauraiacolina@gmail.com (L. Iacolina), aritz.ruiz@ehu.es (A. Ruiz-Gonzalez).

for wild species and their habitats (Trouwborst et al., 2015; Pereira and Navarro, 2015). Increasing populations of some species act as sources for dispersal and (re)colonization, and humans have assisted range expansion by means of active reintroductions (Deinet et al., 2013). Rewilding thus offers intriguing opportunities to investigate contemporary evolution, including traits such as exploratory behaviour (Chapple et al., 2011) that may characterize new arrivals, and the capacities of wild species to respond to changing climatic conditions.

The return of wild species is expected to help restore vital ecosystem processes, including the effects of grazing and browsing, preservation and creation of wetlands, and effects of predation potentially encompassing numerical and behavioural changes in prey species (Deinet et al., 2013; Pereira and Navarro, 2015), suggesting important evolutionary implications for how wild species resume (or assume) their ecological function. This could include potential costs associated with novel infectious diseases (Fernandez et al., 2006). Accordingly, there are diverse views on what constitutes appropriate historical baselines, whether humans should actively reintroduce wildlife, and the acceptance of new species as ecological replacements for extirpated taxa, all of which highlight our incomplete knowledge of ecosystem responses to rewilding (Fernandez et al., 2017).

Given the various interpretations of “rewilding” (Fernandez et al., 2017), we here use a definition from Rewilding Europe (rewildingeurope.com): “Rewilding is a progressive approach to conservation. It's about letting nature take care of itself, enabling natural processes to shape land and sea, repair damaged ecosystems and restore degraded landscapes. Through rewilding, wildlife's natural rhythms create wilder, more biodiverse habitats.” This definition encompasses contemporary evolution and acknowledges that species evolutionary trajectories and community interactions may differ from historical records. In this context, the rewilding of domesticated species may provide an additional example and although not normally considered within the definition of rewilding, de-domesticated species or populations (such as robust livestock breeds) are at times used as the ecological equivalent/replacement of their wild (but extinct) ancestors (e.g. for grazing) (Pereira and Navarro, 2015). Indeed, some species have assumed similar functions after their introduction to new areas, such as reindeer (*Rangifer tarandus*) and moose (*Alces alces*) in their role as grazers and browsers (Lundgren et al., 2017). At times, such introduced species might be seen as making landscapes more biodiverse and wild (Lundgren et al., 2017; Schlaepfer, 2018; Wallach et al., 2018) and the ecosystem effects of removing them can be complex (Gleditsch and Carlo, 2011; Lurgi et al., 2018). Conservation genomic approaches can help us understand the interactions between local ecosystem processes and contemporary evolution. This may be especially relevant for landscapes experiencing (re)colonization by herbivorous and carnivorous species, and thus potentially rapid spatiotemporal changes in processes such as predation and scavenging.

There is considerable discussion about the ecological and evolutionary effects of carnivores, and it has been suggested that further manipulative research is needed to allow more reliable inferences (see e.g., Allen et al., 2017 and references therein). Yet manipulative research of this nature is often controversial. Rewilding processes thus offer important opportunities to investigate the long-term functions of carnivores within the diverse ecosystems of which they are part. Advances in genomics, including next-generation sequencing and use of minimally invasive sources of DNA (e.g., Carroll et al., 2017), combined with comprehensive environmental datasets, high-resolution images from wildlife cameras for individual identification and light-weight instrumentation incorporating Global Positioning Systems technology (Kays et al., 2015) are transforming our understanding of how rewilding shapes wild species and ecosystems, with potential to expand the development and application of tools in conservation genomics (Benestan et al., 2016; Hunter et al., 2018). Correspondingly, conservation genomic techniques, including emerging environmental association studies in landscape genomics (Rellstab et al., 2015) and genomic monitoring aiming at quantifying temporal changes (Carroll et al., 2017), offer new means for testing predictions about rewilding, improving the prospects of evolutionary enlightened management (*sensu* Ashley et al., 2003) and planning.

The potential for rewilding and conservation genomics to offer mutually enhanced benefits warrants further consideration. Firstly, new methods permit rapid advances in understanding contemporary evolution, including local environmental selection (Rellstab et al., 2015) and differential effects of hybridization in various regions of the genome (vonHoldt et al., 2017). This knowledge can help illuminate the extent to which inherent changes in animal behaviour and ecology (evolutionary change, phenotypic plasticity) influence (re)colonization, relative to the impacts of changing landscapes, climates, social attitudes and legislation. Reports of native species increasingly adapting to long-established urban environments (Gehrt et al., 2011) suggest that such range expansion might, at least partially, be due to inherent changes in animal behaviour and ecology.

Range expansion in wild species implicated in rewilding usually results from individual dispersal decisions, not placement into environments deemed suitable by humans. Importantly, however, rapidly changing landscapes could increasingly force species such as large carnivores to occupy more human-dominated landscapes (Chapron et al., 2014; Carter and Linnell, 2016; López-Bao et al., 2017), raising important questions for basic evolutionary science and conservation planning. Rigorous research design accounting for external factors is seldom feasible in landscape-scale ecological and evolutionary research (e.g., Allen et al., 2017 and references therein). Here, rewilding and (re)colonization can contribute to research design increasingly focused on testing *a priori* predictions. Despite the lack of a fully controlled research environment, species dispersal into the mosaic of European landscapes and the ensuing ecological and evolutionary interactions (see e.g., Lesniak et al., 2017; Kołodziej-Sobocińska et al., 2018) will allow testing of a diverse set of predictions relevant across taxa, including the importance of adaptations toward warmer and drier climatic conditions, and degree to which evolutionary changes are contributing to ongoing range expansions. The results could provide vital information for organisms urgently threatened by changing environmental conditions, a situation highlighted in recent reports across vertebrate taxa (Ceballos et al., 2017).

Another example is provided by human-initiated reintroductions where *a priori* predictions can be made and various scenarios investigated by theoretical simulations and later tested with empirical data, for example on the effects of mildly

deleterious alleles at various effective population sizes. Genetic rescue efforts to preserve small populations threatened by inbreeding, such as the planned reintroduction of lynx (*Lynx lynx*) from the Carpathian Mountains to the Dinaric Mountain region (www.lifelynx.eu) follow earlier reintroduction efforts in the 1970s that augmented the Dinaric population's effective size and genetic diversity, followed by a decline (Sindić et al., 2013). Such reintroduction projects offer opportunities for “experimental” research on major questions in ecological and evolutionary genomics, including how genetic distance between populations and transgenerational effects can influence heterosis (Jensen et al., 2018) in wild populations. The combined experience of academic staff and other practitioners can help promote the direct application of genetic results to conservation (Britt et al., 2018) by, for example, improving guidelines for the translocation frequency required to maintain the evolutionary potential of small and isolated populations. For investigations of population changes over time and space, the local ecological knowledge of residents can also help identify population trends and geographical priority areas for monitoring (e.g., Azzurro et al., 2011). Accordingly, conservation genomics can offer important contributions to rewilding efforts for reintroduced or reinforced populations, and how to manage these in an evolutionary enlightened and cost-effective manner.

In this perspective article we examine four species involved in (re)colonization and/or rewilding in Europe, and discuss opportunities for novel research into genomics, evolutionary ecology, and human-wildlife relationships. Our focus is carnivores, which can colonize new areas quite rapidly, and often elicit reactions from humans (no longer used to) sharing their environment with these species (Chapron et al., 2014). We consider species that (1) recolonize former ranges, (2) colonize new regions naturally and expand their historical distribution, (3) represent non-native colonizers (alien invasives), and (4) are critically endangered and subject to human-assisted population restoration (i.e. reintroduction and reinforcement). We also compare their status and capacity for (re)colonization, and note their relevance as examples beyond Europe (Supplemental Table S1).

All our examples concern carnivores and thus a small set of illustrations relevant for opportunities to better connect conservation genomics and ongoing processes of (re)colonization. We primarily aim to provide concrete examples that highlight important knowledge gaps, based on our general research experience and the four carnivore species chosen as case studies. We encourage research design that includes formulation of *a priori* predictions that can be tested by rewilding and (re)colonization processes in the coming years, although it has not been our goal to give detailed prescriptions on research design or methods. As such, we echo Wayne and Shaffer (2016) that our aim is not to present a comprehensive review but to reflect on research ideas and opportunities. Instead, we wish to highlight how genomics and (re)colonization can provide mutual benefits to a broad specter of questions (e.g., behaviour, physiology, hybridization) of interest across taxa.

2. Case studies

2.1. Recolonizing species – the wolf (*Canis lupus*)

The wolf has recently recolonized European ranges including Germany, Denmark, Austria, Hungary, and Switzerland (Deinet et al., 2013; Andersen et al., 2015; Chapron et al., 2014; Boitani et al., 2018), but returns to considerably altered landscapes. Increased proximity to humans, roads and domestic animals could impose new selective pressures (Deinet et al., 2013; Chapron et al., 2014). In some areas, hybridization with domestic dogs (*C. l. familiaris*), at times over extensive areas (Pacheco et al., 2017) might allow rapid acquisition of genetic variation facilitating coexistence with humans, threatening genetic integrity but offering access to additional habitats (Godinho et al., 2011). A possible example is physiological adaptations such as digestion of starch, which has been documented in domestic dogs (Axelsson et al., 2013). Climate change may also provide an additional influence on the patterns of hybridization in many species (Chunco, 2014). Habitat differences across broad ecological regions can influence wolf population genetic structure (Schweizer et al., 2016), and range expansion in this mobile species could facilitate natural experiments on environmental selection. In some species, long-distance migrants might represent bold and inquisitive individuals (Chapple et al., 2011), a behaviour that could help facilitate range expansion. Additional strategies toward increasing available habitat include temporal avoidance. Such behaviour has become well-known in e.g. resident urban coyotes (*C. latrans*) to avoid human activity (Gehrt et al., 2011), and recent research has found that diverse species (Gaynor et al., 2018) including wolves (Barocas et al., 2018) seem to be evading humans by increasing their night-time activity. New genomic and behavioural data could help clarify how human-altered landscapes may be expected to contribute additional viable habitats for wolves and other carnivores (Carter and Linnell, 2016; López-Bao et al., 2017). Key priorities for future research include the possible selection for persistence in human-modified landscapes. These could e.g. be associated with behaviour seeking to avoid humans (Gaynor et al., 2018) and immune responses linked to pathogens connected to human-generated waste (Plaza and Lambertucci, 2017).

2.2. Species expanding their historical range – the golden jackal (*Canis aureus*)

The golden jackal is a native species to southeastern Europe now expanding into additional countries including Poland, Estonia, and Germany (Rutkowski et al., 2015 and references therein, Hoffmann et al., 2018). As the expansion occurs without direct human assistance, it is considered a natural colonization and the species is expected to be treated as native fauna in accordance with European Union law and directives (Trouwborst et al., 2015). The arrival of jackals could nevertheless produce ecological changes in wildlife communities (Arnold et al., 2012; Ivanov et al., 2016; Krofel et al., 2017), and the extent to which jackals may compete with red foxes (*Vulpes vulpes*) or wolves is not well understood. Relative to wolves, smaller

jackal body mass, group size and territories could facilitate its integration into human-dominated areas, as seen for North American coyotes (Gehrt et al., 2011). Rapid jackal range expansion into northern countries is an excellent opportunity to examine effects of temperature and other environmental variables, and clarify the role of mild winters for range expansion and survival (Deinet et al., 2013). The need to understand jackal behavioural and ecological plasticity (Arnold et al., 2012) suggests a model species for investigating climate change effects on range expansion. Important questions for investigation are the possibilities for environmental selection linked to longer, colder winters with deeper snow (Giannatos, 2004; Szabó et al., 2009) associated with the recent expansion into parts of northern Europe. For this and other species enlarging their distribution northward (e.g., Chubbs and Phillips, 2005) or, alternately, southward (e.g., Winkler et al., 2017), it is also relevant to explore the extent to which these processes may be driven by evolutionary and/or environmental change, including climate and habitat conditions. Furthermore, the presence of dog-jackal hybridization with back-crossing to parental species (Galov et al., 2015) raises similar questions concerning adaptation to human environments as those noted above for wolves, whereby the species may acquire novel adaptations via genome regions introduced from dogs, with possible consequences for their distribution, rate of range expansion and ecosystem function.

2.3. Invasive alien species – the raccoon dog (*Nyctereutes procyonoides*)

The raccoon dog is native to South East Asia, South East Siberia and Mongolia (Kauhala and Kowalczyk, 2011) but was introduced, as fur game species, in the early 20th century into several locations of the former Soviet Union (Kauhala and Kowalczyk, 2011; Kauhala and Saeki, 2016). The species subsequently started its northern and western expansion, colonising neighboring countries from introduction sites and by escaping from fur farms (Pitra et al., 2010) and is considered one of the most successful alien carnivores in Europe. Raccoon dogs are now widespread in northern and eastern Europe, and expanding into central Europe and southward (Kauhala and Kowalczyk, 2011). The species may negatively affect native fauna and act as a vector for zoonoses and parasites (Oivanen et al., 2002; Kauhala, 2004; Romig et al., 2006). Conservation genomic tools can help us understand: (a) species population history, as introductions likely occurred from multiple areas of its native range (Pitra et al., 2010; Nørgaard et al., 2017), (b) the high plasticity that allowed colonisation of different environments, (c) how warming climates will influence distribution and population density, as long winters appear to limit their distribution (Helle and Kauhala, 1991) and (d) the potential transmission and impact of zoonoses, by means of metagenomics approaches (Bodewes et al., 2014). A priority research question for the species is to understand what environmental factors may further limit their range expansion. Furthermore, contemporary evolution may be occurring in the form of adaptations to northern environments with colder weather and deeper snow, as noted above for jackals. In contrast, conditions in southern habitats and ongoing climate change could require increased tolerance to warmer and drier habitats. Ongoing range expansion in this species could simultaneously allow comparison of genomes from both colder and warmer environments, plus their native range, to quantify patterns of selection across the genome and the rates of change in different environments. Such information could aid conservation planning, including that for protected areas and sensitive populations of potential prey species, where raccoon dog arrival or population increases could have serious ecosystem implications.

2.4. Population restoration of endangered species – the European mink (*Mustela lutreola*)

The European mink (*Mustela lutreola*), a small semi-aquatic carnivore, is critically endangered and is considered the most endangered mammal in Europe (Maran et al., 2016). Its original range covered most of continental Europe, but less than 5000 individuals now persist in three isolated and declining populations encompassing <3% of its former range (Harrington et al., 2017). Major underlying causes for this population decline are habitat loss and fragmentation, past over-harvest, and the invasion of a dominant competitor, the American mink (*Neovison vison*) (Maran et al., 2016). Legal protection measures and intensive *in situ* and *ex situ* conservation efforts are underway, including habitat restoration, eradication of invasive American mink, prevention of non-natural mortality, captive breeding and population restoration programs (Maran et al., 2016).

Improved genomic information is urgently needed to aid species on the brink of extinction (Maran et al., 2016; Pertoldi et al., 2016), and actively managed species such as this present invaluable research opportunities rarely found in nature. This includes considerations for admixture between human-separated lineages and possible effects from natural introgression, which might be considered an *in situ* conservation strategy (Hamilton and Miller, 2015) but should be carefully examined (Kovach et al., 2016). Addition of new alleles from crossing with the European polecat (*Mustela putorius*) may provide another means of genetic rescue although the evolutionary consequences should be thoroughly evaluated (Cabria et al., 2011). Captive populations can offer highly controlled conditions for examining immediate and long-term effects on the genome from introgression. By providing conditions similar to candidate environments for (re)introduction, and possibly by managing captive populations at candidate sites to monitor survival and reproduction, the most well-adapted individuals and genotypes could be selected, augmenting the opportunity that population reinforcement will help the species resume its historic ecosystem role.

Whole-genome and/or reduced representation approaches, and the development of genome-wide single nucleotide polymorphism (SNP) panels – strategies that could benefit from resources for closely related species (e.g. Peng et al., 2014) – would help resolve how genomes may be altered by demographic declines, and how this influences vital rates and viability in a global change scenario. A research priority is the development and integration of new genomic toolboxes into a multi-disciplinary European mink conservation programme. Efficient and cost-effective SNP panels are important for the

urgently needed pan-European captive breeding strategy (Maran et al., 2016), because the long-term outcome of such programmes is determined by genetic processes (e.g. inbreeding and outbreeding depression, loss of genetic diversity and adaptation to captivity) and requires “portability” of data across laboratories. Genomic, ecological and behavioural research on the disjoint mink populations can help illuminate the beneficial and/or negative effects (e.g. loss of unique adaptations) of potential management actions to attempt genetic rescue of the low-variability Western population (Maran et al., 2016; Carbonell, 2015) and inform integration into a joint breeding programme.

3. Conclusions

Rewilding provides opportunities to test effects of changing environmental conditions across relatively short time scales during wildlife (re)colonization. Considering the known or expected ecological functions of non-native species and populations (Lundgren et al., 2017; Schlaepfer, 2018), research on how changing climates and habitats influence these species can also be informative. Experimental research plays a vital role in evolutionary research and in understanding how wild species respond to shifting environmental conditions. Manipulative experiments with carefully designed case and control populations on the effects of e.g. changing temperatures are standard practice with laboratory organisms such as fruit flies (*Drosophila* sp.) but unlikely with free-living wild species where it is often impractical, unethical or exceedingly expensive. Human perceptions of suitable habitats for carnivores, how these species should behave, and where we should prioritize their conservation may require careful consideration for long-term landscape management (Carter and Linnell, 2016; López-Bao et al., 2017). As depicted in our examples from four carnivore species involved in (re)colonization, genomic research could offer new insights on the ecological roles of carnivores in time and space (Allen et al., 2017 and references therein) and how these may be shifting in rapidly changing landscapes. Such research would likely require, and simultaneously help advance, international collaboration involving standardization of methods and cross-boundary population monitoring and management (Carroll et al., 2017).

Future changes in climate, landscape characteristics and human occupancy will require evolutionary enlightened (*sensu* Ashley et al., 2003) decisions about novel wildlife occurrences and appropriate human responses, probably based on conservation legislation with incomplete guidance for environmental changes not accurately foreseen. It is therefore critically important to learn as much as possible from opportunities for (relatively) experimental study design that is ethically sound, innovative, and based on emerging knowledge from wildlife (re)colonization.

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Appendix A. Supplementary data

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